

Observations on the biology of the endangered stygobiotic shrimp *Palaemonias alabamae*, with notes on *P. ganteri* (Decapoda: Atyidae)

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ABSTRACT

Palaemonias alabamae is endemic to subterranean waters in northern Alabama. Its type locality is Shelta Cave, Madison County, and ostensibly conspecific shrimps have been found in Bobcat and two other caves. Pollution and other factors may have extirpated the shrimp from the type locality. In Shelta Cave the species is smaller than the shrimp in Bobcat Cave and *P. ganteri* in Mammoth Cave, Kentucky. Adult female *P. alabamae* (s.s.) and *P. ganteri* are larger than males. Female *P. alabamae* with visible oocytes or, rarely, attached ova, were observed from July through January in Shelta Cave. Each female there produces 8 to 12 large ova, whereas females of the population in Bobcat Cave produce 20 to 24 ova, and *P. ganteri* produces 14 to 33 ova. Plankton samples taken in Shelta and Mammoth caves yielded nothing identifiable as zoea or postlarvae. *Palaemonias alabamae* and *P. ganteri* usually feed by filtering bottom sediments through their mouthparts, but both sometimes feed upside down at the water's surface. Although there is some overlap, the compositions of the aquatic communities in Shelta and Mammoth caves differ, and there are some major differences among the Alabama shrimp caves. The stygobiotic fish, *Typhlichthys subterraneus*, is a known predator on *P. alabamae* in Shelta Cave.

Key words: cave shrimps, *Palaemonias alabamae*, *P. ganteri*

INTRODUCTION

The shrimp family, Atyidae, is a large, cosmopolitan group of decapods that, in the Americas, contains nine described stygobiotic species (Holthuis 1956; Hobbs et al 1977). Two of them are found in caves of the United States: *Palaemonias alabamae* Smalley, 1961, occurs in subterranean systems in northern Alabama, where its type locality is Shelta Cave in Huntsville, and *Palaemonias ganteri* Hay, 1902, occurs in underground waters in the Mammoth Cave area of central Kentucky, where its type locality is Roaring River in Mammoth Cave. Unfortunately there is evidence of reductions in the numbers of the aquatic stygobionts in Shelta Cave (Lee 1987; Hobbs and Bagley 1989), which has been subjected to an influx of pollutants, including cadmium and the pesticide dieldrin (McGregor et al 1997:33, 56). Elevated levels of cadmium have also been reported for Bobcat Cave, in which *Palaemonias* occurs (McGregor et al 1997:33; McGregor & O'Neil 2000:9, 26). Cadmium has been shown to accumulate in much higher concentrations in the tissues of a stygobiotic crayfish species that occurs in Shelta Cave than in the tissues of a stygophilic species that also occurs there (Dickson et al 1979). This was attributed to the greater longevity of the stygobiont as reported by Cooper (1975), and Cooper and Cooper (1976, 1978a). Other studies on the

toxicity of cadmium to crayfishes were reported by Wigington and Birge (2007).

An additional factor that has certainly had an impact on Shelta's aquatic community is abandonment of the cave by a longtime maternity colony of the grey bat, *Myotis grisescens* Howell, 1909, which contributed guano and occasional dead individuals to the community's trophic inputs (Cooper 1975:45-48). Grey bats were present during many of our trips to the cave, including in July 1975, but apparently vacated sometime in the later 1970s. On our final trip to the cave, during 12-17 July 1975, we spent 34 hours inventorying the aquatic fauna. In West Lake, the populations of all crayfishes were in very good shape, but no shrimp were observed. Our sighting of two shrimp on 24 November 1973 was the last reported for Shelta Cave. Thus, it is possible that *P. alabamae* has been extirpated from the type locality. On the other hand, *P. ganteri* was once assumed extinct (Lisowski and Poulson 1981; Lisowski 1982), but later intensive field work resulted in its "rediscovery" (Lisowski 1983). At any rate, because of its rarity, or possibly its extirpation from Shelta Cave, we have decided to publish our baseline observations on some aspects of the biology of *P. alabamae* (s.s). Both it and *P. ganteri* are now considered federally endangered species.

MATERIALS AND METHODS

During the period 24 August 1963 through 17 July 1975 we made 78 research trips into Shelta Cave, spending a total of approximately 580 hours there (Cooper 1975). Although most of our efforts were devoted to studies of the three stygobiotic crayfishes that inhabit the cave, during some of our trips we also collected information on *P. alabamae*. In addition, at times during this period we collected and made observations on the biota of two of the other caves where shrimp are now known to occur (Cooper & Cooper 1974; McGregor et al 1997; Rheams et al 1992).

We maintained a small colony of 9 to 13 *P. alabamae* in a large plastic pool within Shelta Cave for a little over five months during the winter of 1968-69. Measurements of preserved specimens were made to the nearest 0.1 mm with a Helios dial caliper. The standard length measurement for shrimp is postorbital carapace length (PCL), measured from the level of the posterior rim of the orbit to the center of the proximal margin of the carapace. The length of the rostrum (RL) usually is not included in such measurements, but can itself be informative. Total length (TL) of these shrimp is difficult to accurately assess, since the abdomen is very pliable and has a normal flexion. Nevertheless, TL measurements were included in this study in order that (1) potential sexual dimorphism related to comparative abdomen length could be assessed, and (2) the series of *P. alabamae* could meristically be compared with a series of *P. ganteri*, whose TLs (exclusive of RLs) were reported by Barr and Kuehne (1971), and with *Palaemonias* from Bobcat Cave, whose TLs (including RLs) were reported by McGregor & O'Neill (2000) and McGregor et al (1997).

RESULTS AND DISCUSSION

Occurrence and Abundance

Palaemonias alabamae was “apparently first collected by T. L. Poulson,” who found a single female in Shelta Cave on 13 July 1958 (Cooper 1975:129). Biologists from Tulane University and their colleagues then made three visits to the cave and acquired the 18 specimens that constituted the type series for Smalley’s (1961) description. The holotype (USNM 107028) and six paratypes (USNM 107029) are at the National Museum of Natural History, Smithsonian Institution, but the whereabouts of the rest of the Tulane collection are unknown (N. Rios, pers. comm.). The first specimens we found were two females collected on our initial trip to the cave on 24 August 1963. Table 1 is a chronological summary of our *P. alabamae* sightings there in 30 of our trips between 1963 and 1973. McGregor & O’Neil (2000:35, 38) provided chronological summaries for all *Palaemonias* observations in Bobcat Cave on the Redstone Arsenal, Madison County, from December 1990 through September 2000.

Table 1 - Chronological summary of *P. alabamae* observations in Shelta Cave, Alabama, 1963 through 1973.

1963
24 Aug. -- 2 ♀. 22 Dec. -- “plentiful”
1964
18-19 Oct. -- 7. ? Dec. -- 5. 3 Jan. -- 8 ♂, 10 ♀ (1 ovigerous); many others observed.
1966
18 Sep. -- “plentiful.” 20 Nov. -- 3.
1968
27 Jul. -- 12. 23 Sep. -- 2. 1-3 Nov. -- 15. 8-9 Nov. -- 9. 7-10 Dec. -- 25.
1969
18-20 Jan. -- 5. 10 Jul. -- 3. (1 ovigerous ♀). 12-14 Sep. -- 1.
1970
11 Feb. -- 1 ♀. 26-28 Nov. -- 3
1973
24 Nov. -- 2

Palaemonias was believed endemic to Shelta Cave (Cooper 1966, 1967, 1968a, 1974, 1975; Cooper & Cooper 1966, 1971) until in 1973 William Torode discovered shrimp in Bobcat Cave (Cooper & Cooper 1974). We visited the cave with him on 23 November 1973 and, in residual pools, found 10 *Palaemonias*, several *Cambarellus* (*Aviticambarus*) *jonesi* Hobbs and Barr, 1960, and a number of *Typhlichthys subterraneus* Girard, 1860. In 1990, under terms of a cooperative agreement with the U. S. Fish and Wildlife Service, investigators from the Geological Survey of Alabama (GSA) began conducting multidisciplinary field studies in and around Shelta, Bobcat, and other caves in Madison County, with *Palaemonias* as their primary focus. Their work produced a wealth of data relating to the biota and other aspects of those particular caves (McGregor et al 1997; McGregor & O’Neill 2000; Moser & Rheams 1992; Rheams et al 1992, 1994). In October and November 1991, Karen Rheams, Stuart McGregor and Randall Blackwood found *Palaemonias* at a third locality, the extensive Hering-Glover cave system in eastern Madison County (Rheams et al 1992:66). Rheams et al (1994:58) additionally reported that Torode and others had in November 1991 observed shrimp in Brazelton Cave, identified by Graham (1969) as a possible western resurgence for the Hering-Glover system. They later confirmed the occurrence of *Palaemonias* in Brazelton Cave, and reported a connection between it and the Hering-Glover system (McGregor et al 1997:18). Recently, Kuhajda (2006) reported finding *Palaemonias* in Muddy Cave, south of Huntsville, and cave shrimps of undetermined taxonomic status have been found in three caves in northwestern Alabama (B. Kuhajda, pers. comm.).

Palaemonias Habitats

Shelta Cave -- The type locality of *P. alabamae* is located in Huntsville, Madison County, Alabama. It is an active drainage conduit of considerable volume in which large quantities of water are "stored" for many months every year. There are no incoming or outgoing streams, but at least some of the cave's continuous input of water is of seasonal meteorological origin in the zone of aeration. In winter, heavy precipitation in the recharge areas results in rapid upwelling of water into the aquifer, the water table experiences a dramatic rise, and the result within the cave is prodigious flooding. Spring and early summer rains maintain relatively high but fluctuating and generally receding water levels, and as precipitation decreases in late summer and fall the water table recedes by lateral migration and accessible water disappears from most of the cave (Cooper 1975:29). However, in fall and early winter there is a permanent, shallow perched lake (West Lake) in the extreme western part of the cave (Miller Hall), which maintains fairly constant levels and feeds a perennial stream that sinks before reaching the main cave. When standing water was essentially absent from the rest of the cave, we found that large numbers of aquatic stygobionts "retreated" to West Lake. The lake is probably fed by movement of groundwater through the porous limestone, since there are only what seem to be minor inputs of meteorological origin at this time (Cooper 1975:102-110). The resurgence for Shelta Cave's waters appears to be Brahan Spring (Moser & Rheams 1992:31-32; Rheams et al 1994:43), which is impounded in a park northeast of Drake Avenue, about 3.5 air km south of Shelta Cave.

For descriptions of the cave's size, structure, hydrologic cycles, fauna, ecology, physicochemical characteristics, and history, with maps and photographs, see Cooper (1966, 1968a, 1974, 1975), Cooper & Cooper (1971, 1976, 1978a, b), French (1968), Hobbs & Bagley (1989), Johnston (1933), Jones & Varnedoe (1968), Moser & Rheams (1992), Peck (1989), Rheams et al (1992), Tarkington et al (1965), Torode (1973), Varnedoe & Lundquist (2005), Veitch (1967), and Wilson (1969). Bobcat Cave -- This cave is located on the Redstone Arsenal about 13 air km southwest of Shelta Cave. It is not as voluminous as Shelta, but their hydrologic cycles are virtually identical, with lentic waters that experience heavy seasonal rises and drops. During periods of low water, only small residual pools remain and, as in all of Shelta Cave except the West Lake, the water table at this time lies below the accessible levels of the cave. For additional information, including maps and photos, see McGregor et al (1997), McGregor & O'Neill (2000), Moser & Rheams (1992), Rheams et al (1992, 1994), and Varnedoe & Lundquist (2005).

The Hering-Glover System -- The caves that make up this system are located between Keel and Troy mountains in southeastern Madison County, southwest of the town of Gurley. The Hering-Glover system is very dif-

ferent from Shelta and Bobcat caves, being an open system that is mainly a fairly narrow, winding phreatic tube with some side passages and alcoves. During seasonal spates the entrance may be nearly sumped, and the lotic outgoing water then becomes a rocky surface stream that passes under a highway before sinking into Glover Sink Cave.

Our observations in 1965, 1967, and 1968, and published information from 1929 (Johnston 1933), 1953 (Malmberg & Downing 1957), 1968 (Graham 1969), and 1990- 1992 (Rheams et al 1992), show that this system floods in late winter and early spring, the waters begin to recede in mid-summer, and lowest water levels are present from late summer through fall and into early winter. Some fluctuations occur at various times in response to heavy surface precipitation. Even during extreme drawdowns, however, there are lentic bodies of water in the caves, varying from small, shallow residual pools to base-level "lakes" (Rheams et al 1992). The water table is often broadly exposed in parts of the system and, as with Shelta and Bobcat caves, it would appear to be underlain by an extensive aquifer inaccessible to investigators.

When we made our second trip to Hering Cave, on 30 December 1965, the scoured floor of the main passage was dry and sandy, with some limestone and chert pebbles. The only accessible water there was a number of small residual pools that contained the stygobiotic fish, *T. subterraneus*, the stygobiotic crayfish, *Orconectes australis* (Rhoades, 1941), the stygobiotic isopod, *Caecidotea birenata birenata* (Steeves, 1963), the stygophilic crayfish, *Cambarus (Erethicambarus) tenebrosus* Hay, 1902; and the stygophilic fish, *Cottus carolinae* (Gill, 1861). No shrimp were observed.

Graham (1969:11, corrected) observed that the resurgence for the Hering-Glover system "is not definitely known although it may be Brazelton Cave (AL 337), 4000 feet northwest of Glover Cave and on the other side of the mountain." The waters of Brazelton Cave apparently rise and fall on the same seasonal schedule as those of the Hering-Glover system. On 8 November 1990, and 30 October and 13 November 1992, Rheams et al (1992) found pools and lakes varying from 0.3 to 4.8 m deep in the cave. On 23 July 1992, however, they found the entrance sumped, and flowing from it was a swift stream about 1.2 m deep.

Not only is the Hering-Glover system of interest because of its basically lotic habitat, but also because the shrimp's occurrence there places it in a different physiographic and geologic setting. Shelta and Bobcat caves are within the eastern periphery of the Highland Rim, and both are developed in the Warsaw Limestone and the underlying Fort Payne Chert (Cooper 1975, Rheams et al 1994). Keel and Troy mountains, though, are outliers of the Jackson County Mountains, thus part of the dissected rim of the Cumberland Plateau, and the caves there are developed in the Monteagle Limestone. For additional

information on the Hering-Glover system, including maps of the caves, see Graham (1969), Johnston (1933), Jones & Varnedoe (1968), McGregor & O'Neil (2000), McGregor et al 1997), Rheams et al (1992, 1994), Tarkington et al (1965), and Wilson (1969).

Molting and Potential Longevity

No direct data are available on growth or longevity in *P. alabamae*, but some information on molting has been obtained, and limited inferences on longevity can be made from our studies of Shelta's other stygobiotic decapods.

On 3 November 1968, a female with a postorbital carapace length (PCL) of 5.4 mm and very early oocytes visible through the carapace was found in the process of molting in the shrimp pool, but the animal neither completed nor survived the process. The exuvium of another individual was found on 10 December 1968, along with seven live animals. This is the only direct molting information we obtained, and it suggests at least a winter molt for some adults. Indirect evidence of a summer molt was obtained from an adult female (PCL 5.3 mm) collected on 10 July 1962, which had obvious calcareous concretions on many parts of the body. These appeared to be similar to the molting nodules that Jefferies (1964) described on the epigean palaemonid shrimp, *Palaemonetes varians*, and could indicate relative molting condition. These nodules are most numerous immediately following molting, after which they decrease in number.

We initially were tempted to conclude that *P. alabamae* has a longevity of one year, with the adult class diminishing in abundance from later winter into early summer. This, however, would be inconsistent with our current knowledge concerning the longevity of the other stygobiotic decapods in Shelta Cave (Cooper 1975; Cooper and Cooper 1978a). Additionally, it would require relatively rapid growth, which is also at odds with what we now know of the rate of growth of the other stygobiotic decapods (Cooper 1975; Cooper & Cooper 1976, 1978a; Culver 1982). It is more likely that the broad habitat expansion that occurs during high water results in greatly decreased population density, which renders these small, largely transparent animals less conspicuous than they are during low water levels (Cooper 1975). When habitats were compressed, population densities increased and shrimp were found in shallow residual basins.

One of the stygobiotic crayfish found in Shelta Cave, *Orconectes (Orconectes) sheltae* Cooper & Cooper, 1997, is a diminutive species endemic to the cave. This crayfish has a seasonal and spatial occurrence almost identical to that of *P. alabamae* (Cooper 1975; Cooper & Cooper 1997). Like the shrimp, the crayfish produces only 8 to 12 ova, and in proportion to adult female body length its hatchlings, which are about the size of an adult shrimp, are suspected to be the largest found in any crayfish species (Cooper 1975; Cooper and Cooper 1997). From direct growth and size data, we estimated the lifes-

pan of *O. (O.) sheltae* to be from 10 to 20 years (Cooper 1975:314; Cooper and Cooper 1976; Cooper and Cooper 1978a). One specimen that we had permanently marked was recaptured more than four years after its initial capture, and still had not approached the maximum total carapace length known for the species. In our opinion, a longevity of 10 to 15 years would not be unrealistic for *P. alabamae*.

Leitheuser & Holsinger (1983:2-30) reported for *P. ganteri* that "Information has also been obtained on age and growth rates through observations on aquarium specimens. Growth is slow and variable among individual shrimp. Based upon information such as this, the life span of the shrimp has been estimated to be 10 to 15 years." Based on data from laboratory cultures, Dickson & Holsinger (1981:45) suggested that the life span of the stygobiotic amphipod, *Crangonyx antennatus*, "may extend from 8 to 10 years."

Comparative Sizes, Sexual Dimorphism, and Sex Ratios

Smalley (1961:129) said that *P. alabamae* may be distinguished from *P. ganteri* by features that included its "smaller size" and "shorter rostrum," but provided no data other than noting that the RL of *P. alabamae* constitutes two-thirds of its PCL. Our measurements of both species showed that the abdomen averages about 71 percent of total length, which enabled us to extrapolate probable PCLs for the *P. ganteri* data. Smalley (1961:129) reported a range of 4.2 to 5.9 mm PCL for 19 adult *P. alabamae*. The range in our sample of 34 adults from Shelta Cave was 4.1 to 5.9 mm (mean = 5.0 mm) PCL. Abdomen lengths of our adults ranged from 10.1 to 14.2 mm (mean = 12.1 mm), and total lengths (excluding rostrum) from 14.5 to 20.0 mm (mean = 17.1 mm). Our measurements, and those we obtained or extrapolated from Barr and Kuehne (1971), support Smalley's statement for the Shelta Cave population of *Palaemonias* (Table 2), which was the only population known at the time the species was described. Cooper and Cooper (1974) reported that specimens from Shelta Cave were smaller than those from Bobcat, but provided no comparative measurements. PCL measurements of Bobcat Cave specimens are not available, which is also true of specimens from the Hering-Glover population. McGregor et al (1997:46) listed total lengths, including rostrum, of ca. 83 presumed adults or subadults, ranging up to 29.4 mm. Considering that the greatest total length, including rostrum, in 34 adult *P. alabamae* from Shelta Cave was 24.5 mm, these data provide some quantitative support for the idea that the Shelta shrimp are considerably smaller than those in Bobcat Cave.

The PCL of *P. ganteri* averages only 0.6 mm greater than that of *P. alabamae* from Shelta, but its TL averages 2.2 mm greater. Male *P. ganteri* average 0.5 mm greater in PCL and 1.3 mm greater in TL than male *P. alabamae*, while females of the former average 0.7 mm greater in PCL and 2.9 mm greater in TL than females of the latter.

Table 2 - Comparative measurements (mm) of adult *P. alabamae* from Shelta Cave and *P. ganteri* from Mammoth Cave; some totals include unsexed individuals. N/A = data not available.

<i>P. alabamae</i>	<i>P. ganteri</i>
Postorbital carapace length	
males: R = 4.1-5.9 (mean = 4.5; n = 13)	R = 4.1-5.8 (mean = 5.0; n = 7)
females: R = 4.1-5.9 (mean = 5.3; n = 19)	R = 5.2-6.7 (mean = 6.0; n = 14)
totals: R = 4.1-5.9 (mean = 5.0; n = 34)	R = 4.1-6.7 (mean = 5.6; n = 22)
Total length without rostrum	
males: R = 14.8-18.3 (mean = 16.0; n = 13)	R = 14.0-23.0 (mean = 17.3; n = 7)
females: R = 15.5-20.0 (mean = 17.8; n = 19)	R = 17.9-23.0 (mean = 20.7; n = 14)
totals: R = 14.5-20.0 (mean = 17.1; n = 34)	R = 14.0-23.0 (mean = 19.3; n = 22)
Abdomen length	
males: R = 10.1-13.0 (mean = 11.4; n = 13)	N/A
females: R = 10.9-14.2 (mean = 12.6; n = 19)	R = 12.7-14.9 (mean = 13.8; n = 4)
totals: R = 10.1-14.2 (mean = 12.1; n = 34)	R = 12.7-14.9 (mean = 13.8; n = 4)
Rostrum length	
males: R = 2.9-4.3 (mean = 3.4; n = 10)	N/A
females: R = 3.1-4.5 (mean = 3.8; n = 17)	R = 4.4-5.3 (mean = 4.7; n = 4)
totals: R = 2.9-4.5 (mean = 3.6; n = 29)	R = 4.4-5.3 (mean = 4.7; n = 4)
Percent rostrum length of postorbital carapace length	
males: R = 62.0-86.0 (mean = 74.2; n = 10)	N/A
females: R = 57.4-78.4 (mean = 69.4; n = 17)	R = 75.4-102.0 (mean = 85.0; n = 4)
totals: R = 57.4-86.0 (mean = 70.7; n = 29)	R = 75.4-102.0 (mean = 85.0; n = 4)

Thus, *P. alabamae* is measurably smaller than *P. ganteri*, and at least the females of the latter (and probably the males) have a longer rostrum than all *P. alabamae*.

Sexual dimorphism in size is evident in both species. Adult female *P. alabamae* average 1.8 mm longer in TL and 0.8 mm longer in PCL than males. Abdomen length averages 1.2 mm longer in females than in males. Adult female *P. ganteri* average 3.4 mm longer in TL and 1.0 mm longer in PCL than males. *Palaemonias alabamae* also shows slight sexual dimorphism in absolute length of the rostrum. The female rostrum in our sample averages 0.4 mm longer than the male rostrum. Expressing RL as percent of PCL, however, shows that males average about 4.8% greater than females, which is due to the greater average PCL of females (♂ mean = 4.5, ♀ mean = 5.3). These differences are not an allometric effect, since the males at the low and high extremes of the range both measured 5.0 mm PCL, and the female extremes differed only slightly. In a total of 34 *P. alabamae* examined from Shelta Cave, there were 21 females, 13 males. The only sample large enough (n = 18) to provide significant information on the sex ratios at any given time is the one made on 3 January 1964, which consisted of 10 females and 8 males. Smalley (1961) reported that the same number of shrimp in an 18 August 1960 sample consisted of 11 males and 7 females. In both these collections combined, there are 19 males, 17 females. Barr & Kuehne (1971) reported that two collections of *P. ganteri* from Mammoth Cave contained 12 females, 7 males.

Reproduction

In Shelta Cave, *P. alabamae* with highly visible internal oocytes, or on rare occasions with externally attached ova, were found in every month in which numbers of shrimp were seen, which was from July through January. A female measuring 9.8 mm PCL, found on 24 August 1963, contained 8 oocytes that measured from 0.6 to 0.8 mm long, and on 3 November 1968 an uncounted number of oocytes measuring about 1.0 mm long was observed in a female measuring 5.2 mm PCL. Such medium-to-large oocytes, considered late stage or nearly so, were also seen in a female on 13 September 1968, in four on 18 and 19 October 1969, in three on 3 and 8 November 1968, and in one on 8 December 1968. Smaller, earlier stage oocytes were observed in a female on 3 November 1968. Despite the not infrequent presence of advanced oocytes, only two specimens bearing extruded pleopodal ova were found in Shelta Cave. A female measuring 5.8 mm PCL taken on 3 January 1964 had 9 such ova, measuring 1.0 X 1.2 mm, along with several remnant chorions. A second female, measuring 5.0 mm PCL, taken on 10 July 1969 and placed in the shrimp pool, had 4 attached ova measuring 0.9 X 1.4 mm when examined alive several days after capture (see Cooper 1975:146, Fig. 22). An equal number of ova had been present, however, when the animal was captured, but were lost in the habitat. It thus appears that *P. alabamae* in Shelta Cave produces from 8 to 12 ova per female. Rheams et al (1994:63) inadvertently reported that Cooper (1975) found individual

shrimp in Shelta Cave that “carried from four to 30 ova each,” and this error was repeated in the recovery plan (USFWS 1997) and in the five-year followup report (USFWS 2006). It would further appear, considering that the female collected on 24 August 1963 contained 8 large oocytes in the ovary, that little if any resorption of additional oocytes occurs in females that actually extrude eggs. We know little, however, about the number of females in the population that complete the process, although late-stage oocytes were observed from late August through December. Our research on the stygobiotic crayfishes of the cave produced clear evidence that, while many females contain late stage internal oocytes, only a very few of the largest females actually produce successful clutches of ova or young (Cooper 1975; Cooper & Cooper 1978a, b). Resorption in these crayfishes is a common phenomenon.

For Bobcat Cave, Cooper & Cooper (1974) reported that ovigerous females had been found in September and October, and noted that in Shelta “females appear to produce fewer ova” than do females in Bobcat, but provided no data. Rheams et al (1992:68, 70) reported that “Cave shrimp with attached ova were observed in Bobcat Cave during May (a single, very large specimen with very large eggs observed May 25, 1992), July (an unknown number of the 51 individuals observed on July 22, 1991), August (3 of 13 individuals observed on August 21, 1991), and October (4 of 30 individuals observed on October 28, 1991). These individuals were noted to carry 20 to 24 eggs each.” Except for the “very large specimen with very large eggs” observed in May, this general reproduction schedule appears to be similar to that observed in Shelta.

However, the notable fecundity of *Palaemonias* in the Bobcat Cave population far exceeds that in the Shelta Cave population. Not only is the number of ova per female more than twice the number of advanced oocytes (and attached ova) observed in or on Shelta females, but ostensibly far more females were observed carrying ova. The greater number of ova could be attributable to the larger size of the Bobcat Cave shrimp, but this does not explain the greater number of females apparently completing the reproductive process. Analysis of factors that could account for this putative disparity in fecundity, between two geographically close populations of what has been determined to be the same species, will have to await the results of future studies. It should be noted that only a few of the GSA studies distinguished between visible internal oocytes or ovarian ova, and extruded pleopodal ova. Thus, potential resorption of oocytes cannot be evaluated.

In the Mammoth-Flint Ridge system, ovigerous *P. ganteri* have been collected or observed in every month except February, March, and July (Barr & Kuehne 1971; Cooper 1975; Holsinger & Leitheuser 1982; Leitheuser et al 1985; Poulson 1964; Poulson & Smith 1969). One of the four specimens collected by Barr in August 1965 (Cooper 1975) measured 5.2 mm PCL and had 14 at-

tached ova, which measured about 1.0 X 1.4 mm each. A series of seven ovigerous females reported by Barr and Kuehne (1971), taken on 13 May 1962, measured from 20 to 22 mm TL (mean = 20.9 mm), which translates to ca. 5.2 to 6.4 mm PCL (mean = 6.1 mm), and had from 14 to 33 attached ova.

An additional female reported by the same authors, collected on 13 October 1961, measured 23 mm TL (6.7 mm PCL) and had 15 attached ova. Barr & Kuehne (1971) did not include ova measurements, but did provide weights of each of the egg masses on the eight ovigerous females. The much greater weight of October eggs led Barr & Kuehne (1971:86) to suggest “that peak egg production occurs in later winter or early spring and eggs are carried into or through summer.” They added, “We do not know when the eggs hatch and young shrimps join the population, but presumably this occurs between later summer and winter.” It should be observed that a period of larval development of unknown duration may well separate the time of eclosion and the time of appearance of “young shrimps” in the population (see following “Development” section).

In the two ovigerous *P. alabamae* reported above, ovum length was 1.2 and 1.4 mm, or 20.7 and 28.0% of female PCL (6.0 and 8.1% of TL). In the single *P. ganteri* for which this datum is available ovum length was 1.4 mm, or 26.9% of female PCL (7.8% of TL). It thus appears that *P. alabamae* in Shelta Cave produces only one-third to one-half as many ova (8 to 12) as does *P. ganteri* (14 to 33), although the ova are of comparable size, and that *Palaemonias* in Bobcat Cave produces numbers of ova (20 to 24) that are nearly comparable to the numbers produced by *P. ganteri*. No measurements of ova from Bobcat Cave shrimp are available.

Development

The ova of the ovigerous *P. alabamae* taken in January exhibited midsagittal cleavage and appeared close to eclosion, and several empty chorions were adjacent to them, which would indicate hatching at that time. The slightly longer ova of the smaller July female were not noticeably differentiated, being generally amorphous envelopes of pale, yellow-white yolk. Based on just these few observations, egg laying could occur during medium and falling water levels in mid-summer, with an incubation period of about six months before hatching and emergence. Juberthie-Juneau (1974) reported that incubation in the stygobiotic European atyid, *Troglocaris anophthalmus* (Kollar, 1848) requires 7 to 8 months, but takes only 20 to 35 days in the larger epigean atyid, *Atyaephyra demaresti* (Millet, 1832). The ova of an ovigerous *P. ganteri* collected in August 1965 showed clear polarity and obvious development, with white, well-developed larvae at one pole, deep yellow-orange yolk at the other (Cooper 1975).

Nothing is known of the post-hatching “stages” in either *P. alabamae* or *P. ganteri*. Our plankton collec-

tions and silt samples from Shelta Cave produced nothing identifiable as shrimp zoea or postlarvae, and as far as we know there have been no collections of these early life stages in *P. ganteri*. Barr and Kuehne (1971:83-85) remarked that, in Mammoth Cave, "The most striking feature revealed by analysis of plankton tows is the low density of organisms." Juberthie-Jupeau (1969) reported that larval development in *T. anophthalmus* consisted of five intermolt stages.

In one of the few such studies yet made of an American stygobiotic shrimp, Dobkin (1971) studied the development of larvae from a single female of the palaemonid, *Palaemonetes cummingsi*, from Squirrel Chimney, Florida. The results of the study, conducted in the laboratory at 22-24°C, showed that this species goes through three intermolt "stages" prior to postlarval metamorphosis. The female apparently was carrying from 30 to 35 ova. The entire development period, from early egg to postlarva, required a maximum of 42 days. Based on extensive collections of various life stages of the stygobiotic palaemonid, *Palaemonetes antrorum* Benedict, 1896, which is endemic to the Edwards Aquifer in Texas, Strenth et al. (1988) reported three zoeal and two postlarval stages.

Considering that the incubation period for *P. alabamae* ova appears to be similar in duration to that of *T. anophthalmus*, and much greater than that of the laboratory-reared *P. cummingsi*, we consider it likely that the larvae and postlarvae of *Palaemonias* are considerably larger and much slower growing than those of *P. cummingsi*. To date, however, few direct observations have been made in support of this contention. In addition to being a member of a different caridean family, the palaemonid would seem to be a less highly adapted (i.e., more recent) stygobiont than the atyids. Dobkin (1971: 296) observed that its development "is remarkably like that" of *Palaemonetes paludosus* (Gibbes, 1850). The latter, a large epigean palaemonid common in fresh waters of the eastern United States, is considered to be the closest relative of *P. cummingsi* (Franz 1982: 108). Although these two species are so similar in development, including in the duration of the larval period, the smaller stygobiont still produces larger larvae and postlarvae, and generally fewer but larger ova (with respect to female size), than its epigean relative.

In summary, it appears that *Palaemonias* and the few other stygobiotic atyids for which data are available display a general reproductive strategy that has become evident across a broad spectrum of highly-adapted stygobionts, both invertebrates and vertebrates. This includes the production of fewer and larger ova (thus young), and longer incubation periods than are seen in epigean relatives. These are adaptive responses to life in relatively predictable, food-limited environments, in which a survival premium is placed on smaller populations and "fitter" offspring. The stygobiotic atyids probably also display delayed maturity and reproduction, longer larval development periods, and decreased growth rate

with increased longevity, what we have termed a "Me-thuselah Strategy" (Cooper & Cooper 1978a). All these adaptations are evident in Shelta's stygobiotic crayfishes (Cooper 1975; Cooper & Cooper 1976, 1978a,b), but most remain conclusively to be demonstrated in any stygobiotic shrimp.

Feeding and Other Behaviors

The observations of Hay (1902:226-227), Giovannoli (1933:620), Barr and Kuehne (1971:85), and Smalley (1961) on certain aspects of the behavior of *P. ganteri* and *P. alabamae* are very similar to our own on the latter species. In Shelta Cave, *P. alabamae* were observed sifting through bottom and other silt. They clasp minute bolts of silt in the opposable brushes of the chelate tips of the first and second pereiopods, and rapidly shift these to be scraped off by their mouthparts. Specimens found in areas floored with bat guano, which analysis has shown to be rich in calories and nutrients (Fenolio et al 2005), had black digestive tracts. Barr & Kuehne (1971:85) remarked that "*Palaemonias ganteri* was observed to strain and filter the bottom sediments through its mouthparts more or less in the same manner described for the Brazilian atyid *Atyoida potimirim* [Müller, 1881] by Müller (1981). The food of these troglobitic shrimps probably consists of microorganisms in the silt." We made no attempt to analyze gut content, or to determine the potential bacterial or other microfloral composition of submerged substrates, but we did qualitatively sample the unicellular eukaryotes that live in the silts ingested by all of Shelta Cave's decapods (Table 3).

On 3 November 1968, a shrimp was found in the stream that flows from West Lake, "fluttering" upside down against the surface tension with its limbs. This was the only occasion on which we found *P. alabamae* in flowing water, where the substrate is low in silt. Our impression of this activity was that it involved feeding (Cooper 1975). Hartnoll (1964:78) reported identical

Table 3 - Unicellular karyotes living in silts ingested by *P. alabamae* in Shelta Cave. Those denoted by asterisk (*) also occur in Mammoth Cave (Gittleson and Hoover 1969, 1970).

Flagellates	
<i>Bodo caudata</i>	<i>Caecomonas crassicauda</i>
<i>Bodo celer</i> *	<i>Gyropaigne lefevrei</i>
<i>Bodo compressus</i>	<i>Monas elongata</i>
<i>Bodo lens</i> *	<i>Monas obliqua</i> *
<i>Bodo minimus</i> *	<i>Rhynchomonas nasuta</i> *
Amebas	
<i>Amoeba guttulata</i> *	<i>Heterophrys glabrescens</i> *
<i>Amoeba vespertilio</i>	<i>Pseudodifflugia gracilis</i>
Ciliates	
<i>Aspidisca andrewi</i>	<i>Cyclidium glaucoma</i>
<i>Chilodonella caudata</i>	<i>Vorticella microstoma</i> *

behavior in the stygobiotic palaemonid, *Troglocubanus jamaicensis* Holthuis, 1963, in a Jamaican cave, and interpreted it similarly, saying that “several were swimming upside down along the surface apparently feeding on floating material.” Lisowski (1983:91) observed *P. ganteri* exhibiting the same behavior in Mammoth Cave.

Our experiences with general movement behavior of *P. alabamae* in Shelta Cave were very similar to those of Hay (1902:226-227) for *P. ganteri*. The shrimp are essentially transparent except for the central thorax, which is opaque enough to be seen. They swim slowly, generally for short distances, by continuous paddling of the pereiopods. The body is held rigid, and they “hover” through the water. We never observed the caudal elements being used for movement, since their only escape response when disturbed was to rise slowly in the water, almost to the surface, and swim off.

Ecological Associates and Relationships

The aquatic community composition of *P. alabamae* habitats differs from that of *P. ganteri* in its macroscopic components, despite some overlap, and there are some differences among the communities in three of the Alabama *Palaemonias* caves (Table 4). *Typhlichthys subterraneus* is the most abundant and significant predator in all four systems, and *Palaemonias* undoubtedly plays a role, perhaps a major one, in its energetics. Although we never observed this fish pursuing shrimp in either Shelta or Bobcat caves, a very large individual collected in Shelta on 20 November 1966 regurgitated an adult shrimp (Cooper 1974, 1975; Cooper and Cooper 1974). Mammoth, Shelta, and Bobcat caves each have a second potential stygobiotic predator -- the fish *Amblyopsis spelaea* DeKay, 1842, in Mammoth and the salamander *Gyrinophilus palleucus* McCrady, 1954, in Shelta and Bobcat -- but they are so comparatively rare (Barr 1967; Barr & Kuehne 1971; Cooper 1968b, 1975) that they are proba-

Table 4 - Macroscopic fauna of aquatic communities in which *Palaemonias* occurs. C = common; R = rare; U = present but abundance unknown; P = presence reported but unverified by voucher specimens.

	Shelta	Bobcat	Hering-Glover	Mammoth
Fishes				
<i>Typhlichthys subterraneus</i>	C	C	C	C
<i>Amblyopsis spelaea</i>				R
<i>Chologaster agassizi</i>				R
<i>Cottus carolinae</i>			C	C
“Ictaluridae”			P ¹	
Salamanders				
<i>Gyrinophilus palleucus</i>	R	R		
<i>Eurycea lucifuga</i>	U	U	U	C
Snails				
<i>Antroselates spiralis</i>				C
Crayfishes				
<i>Cambarus jonesi</i>	C	C	P ²	
<i>Orconectes australis</i>	C		C	
<i>Orconectes sheltae</i>	R			
<i>Orconectes pellucidus</i>				C
<i>Cambarus tenebrosus</i> (s.l.)	R	?	C	C
Amphipods				
<i>Stygobromus exilis</i>				C
<i>Stygobromus fecundus</i>				C
<i>Stygobromus</i> n. sp.	R			
<i>Stygobromus vitreus</i>	R			
<i>Crangonyx barri</i>				C
Isopods				
<i>Caecidotea birenata birenata</i>			C	
<i>Caecidotea birenata whitei</i>				C
<i>Caecidotea stygia</i>				C

¹ Reported by McGregor et al (1997:50).

² Reported by Rheams et al (1992:71, 76; 1994:66).

bly not significant shrimp predators. *Gyrinophilus palleucus*, which does not occur in the Hering-Glover system, is known to feed on crustaceans in other caves (Cooper & Cooper 1968). Leitheuser & Holsinger (1983:25-26) reported, "On several occasions, Leitheuser has observed *Amblyopsis* apparently 'stalking' *Palaemonias ganteri* for periods in excess of one hour in Mystic River."

Larvae of the terrestrial, cave-frequenting salamander, *Eurycea lucifuga* Rafinesque, are aquatic predators on small invertebrates, and have been reported from Bobcat Cave (McGregor et al. 1997:48). Fishes of the genus *Cottus* thrive in caves in the United States and are formidable predators, with a large head and mouth. Lisowski (1983:91) reported *Cottus* feeding on the stygobiotic isopod, *Caecidotea*, in Mammoth Cave. *Cottus carolinus* is common in the seasonally lotic waters of the open Hering-Glover system, but does not occur in the essentially closed lentic waters of Shelta or Bobcat caves. Catfishes of the genus *Ictalurus* are also known predators on cave crustaceans (Relyea & Sutton 1974). However, among Alabama's shrimp caves, ictalurids have been reported only in Brazelton Cave (McGregor et al 1997:50).

One species of stygobiotic crayfish, *Orconectes pelliculus* (Tellkampf, 1844), and the stygophilic *C. (E.) tenebrosus*, are found in Mammoth Cave. Three species of stygobiotic crayfishes occur in Shelta Cave -- *C. (A.) jonesi*, *O. (O.) australis*, and *O. (O.) sheltae*. A few individuals of *C. (E.) tenebrosus* have been found in Shelta, but it is not a prominent member of the community. No interactions of any kind were observed between any of these crayfishes and *P. alabamae*. *Cambarus (A.) jonesi* is the only stygobiotic crayfish that we and others have found in Bobcat Cave, and this is one of but a few known caves inhabited by this species where it does not occur with at least one other stygobiotic crayfish. *Cambarus (E.) tenebrosus* may occur in Bobcat Cave, but is yet to be reported from there by name, although "sighted crayfish" occur in a nearby cave (McGregor et al 1997:48). Rheams et al (1992:71, 76; 1994:66) reported the first and only known record of *C. (A.) jonesi* from the Hering-Glover system, collected in Hering Cave on 14 November 1990. In caves where it occurs, this species is always quite abundant and prominent, but we did not find it among the many crayfish we examined in several visits to that cave, and the putative *C. jonesi* specimen cannot be found.

When we collected in Hering Cave on 30 December 1965 and 15 September 1968, the aquatic community included a number of *Caecidotea b. bicrenata*, including females with ova in their marsupia. Neither *Caecidotea* nor any other aquatic isopod occurs in Shelta Cave, and they have not been vouchered from Bobcat Cave although a "white isopod" was reported there by McGregor et al (1997:80). *Caecidotea stygia* Packard, 1871, and *C. bicrenata whitei* Lewis and Bowman, 1981, are common in the Mammoth Cave system

(Lewis 1982). Two species of stygobiotic amphipods, *Stygobromus vitreus* Cope, 1872, and a new species of this genus being described by J. R. Holsinger (pers. comm.), occur in Shelta Cave. Neither is common, and they appear primarily to be elements of the interstitial fauna, occurring in permanent or transient pools, including in the runoff from a bucket collecting drip water from the ceiling (Cooper 1975:56). Amphipods have not been reported from Bobcat Cave or the Hering-Glover system.

Three species of *Stygobromus* and one species of *Crangonyx* occur in the Mammoth Cave system (J. R. Holsinger, pers. comm.). Isopods and amphipods may be the preferred prey of adult *Typhlichthys* (Cooper & Beiter 1972).

ACKNOWLEDGMENTS

Our gratitude is extended to the National Speleological Society, which gave us permission to conduct research in Shelta Cave and provided grants from the Research Advisory Committee and the Ralph Stone Research Award. The graduate school of the University of Kentucky provided a travel grant and a summer research assistantship. Part of our research was supported by traineeships from the National Science Foundation. For advice and encouragement during our studies in Shelta Cave we thank Drs. T. C. Barr, Jr. and T. L. Poulson, and for lodging during those periods we are very grateful to the late Dr. Walter B. Jones and Hazel Jones of Huntsville and to Dr. John Veitch and Joyce Veitch of Decatur. For assistance in the field we are grateful to J. Carpenter, the late J. E. Cooper, Jr., A. Dobson, the late R. C. Graham, the late F. E. McKinney, S. Peck, J. Reddell, W. Sanborn, W. Torode, and W. W. Varnedoe. Copies of reports on the extensive research of the Geological Survey of Alabama were generously supplied by S. McGregor. J. R. Holsinger provided information on amphipods, as well as reports on the research that he, T. Leitheuser, and colleagues conducted in Mammoth Cave National Park. J. Lewis provided information on isopods, and S. M. Gittleson cultured and identified the protozoa of Shelta Cave silts.

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